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Islands in a desert: breeding ecology of the African Reed Warbler *Acrocephalus baeticatus* in Namibia

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The continental African Reed Warbler *Acrocephalus baeticatus*, like its relative the Seychelles Warbler *Acrocephalus sechellensis*, breeds in isolated patches. We studied the mating system of the African Reed Warbler to see whether this species, like the Seychelles Warbler, shows co-operative breeding. The African Reed Warbler is not polygynous. The majority breed monogamously (88%, $n = 65$), however in 12% of the territories three adult unrelated birds (mostly males) were observed participating in the brooding and feeding of nestlings, suggesting a polyandrous breeding system. Multilocus DNA fingerprinting revealed that the helping bird was unrelated to the pair birds. The percentage of nests with helpers was low compared to rates found in the Seychelles Warbler or Henderson Reed Warbler *Acrocephalus vaughani taiti*. This could be due to the scarcity of potential helpers or to the fact that, although limited, birds still had the opportunity to disperse within a meta-population structure in search of vacant territories. The presence of helpers was associated with increased hatching success due to lower predation rates, but not with increased fledging success. Another possible benefit of helping behaviour in this species could be improved predator detection and mobbing. Nest predation was high and warblers tended to build their nests in the highest, most dense reed patches available in their territory. There was no relation between habitat quality, measured as insect food availability, and the occurrence of helpers.

Co-operative breeding is a reproductive system in which individuals other than the main male–female pair also exhibit parent-like ('helping') behaviour toward young of a single nest or brood. Numerous variations have been identified including helping at the nest by non-breeding offspring that delay dispersal and remain with their parents, and various forms of co-operative polygamy or plural breeding in which more than a single male or female share breeding status within the same social unit. Helping generally consists of feeding nestlings or fledglings, but can also include incubation and nest or territorial defence (Brown 1987). Co-operative breeding, where more birds than just the breeding pair raise the young, occurs in about 3.2% of extant bird species (Sibley & Monroe 1990, Arnold & Owens 1998, Hatchwell & Komdeur 2000), and is mainly restricted to tropical and subtropical regions (Rowley 1976, Dow 1980, Brown 1987, Russell 1989). Numerous studies have identified critical constraints on independent breeding: habitat saturation and population isolation (e.g. Woolfenden & Fitzpatrick 1984, Emlen 1984, Komdeur 1992), high dispersal costs (DuPlessis 1992, Ligon & Ligon 1990, Russell 1999), a shortage of breeding partners (e.g. Emlen *et al.* 1991, Walters *et al.* 1992, Komdeur 1992) and a low probability of successful breeding once a territory has been obtained (e.g. Reyer 1980, Emlen 1982, Stacey & Ligon 1987, Curry 1988).

Warblers in the genus *Acrocephalus* exhibit a large variety of mating systems, ranging from monogamous (Moustached Warbler *Acrocephalus melanopogon*,

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Leisler & Catchpole 1992; Reed Warbler *Acrocephalus scirpaceus*, Hoi *et al.* 1995) through facultatively co-operative (Seychelles Warbler *Acrocephalus sechellensis*, Komdeur 1992; Henderson Reed Warbler *Acrocephalus vaughani taiti*, Brooke & Hartley 1995), to facultatively polygynous breeding (Sedge Warbler *Acrocephalus schoenobaenus*, Borowiec & Lontkowski 1988, Bell *et al.* 1997, Alker & Redfern 1996; Marsh Warbler *Acrocephalus palustris*, Hoi & Ille 1996; Great Reed Warbler *Acrocephalus arundinaceus*, Dyrcz *et al.* 1994; Australian Warbler *Acrocephalus australis*, Welbergen *et al.* 2001). The occurrence of each mating system in these species is associated with factors such as migration possibilities (Brown 1987), habitat quality (Hoi *et al.* 1995, Komdeur 1992), habitat saturation (Komdeur 1992, 1995), intra-specific competition (Hoi *et al.* 1995) and predation (Hoi & Winkler 1988, Ille & Hoi 1995). In areas with low intra-specific competition, male warblers show a higher tendency to become polygynous, to produce more offspring (Hoi *et al.* 1995). The same is true for areas with high predation risk. Through polygyny males distribute their offspring between different nests thereby reducing predation risk (Hoi & Winkler 1988). In the Seychelles Warbler (Komdeur 1992) and the Henderson Reed Warbler (Brooke & Hartley 1995), both of which occur on isolated oceanic islands, co-operative breeding is known to be adaptive.

The Seychelles Warbler is confined to three small islands in the Indian Ocean and shows co-operative breeding within family groups. Habitat saturation is the main cause of juveniles staying as helpers. Philopatry is advantageous under saturated conditions through increased indirect fitness benefits (Stacey & Ligon 1987, 1991, Waser 1988, Komdeur 1992). Co-operative breeding in the Seychelles Warbler occurs in approximately 31% of territories (n = 113), depending on habitat quality (Komdeur 1992). Older offspring of the breeding pair remain in their natal territory and help raise putative full-siblings, as long as they have no opportunity to establish territories of their own of equal or higher quality than their natal territory (Komdeur 1992, 1994a, 1994b). In the Henderson Reed Warbler, co-operative breeding occurred in 36% of the observed territories (n = 8), comprising three birds participating in rearing young (Brooke & Hartley 1995). These 'helpers' were unrelated to the breeding pair. They may have helped to gain breeding experience or breeding opportunities with a member of the breeding pair in a subsequent breeding attempt, especially after the clutch of the present breeding pair failed.

In contrast, co-operative breeding does not occur in the six *Acrocephalus* species studied in temperate regions (Leisler & Catchpole 1992, Hasselquist *et al.* 1995, Alker & Redfern 1996, Schulze-Hagen *et al.* 1996, Welbergen *et al.* 2001), although there is some evidence for extra-male parental care in the Moustached Warbler, *Acrocephalus melanopogon* (Fessl *et al.* 1996). Co-operative breeding in *Acrocephalus* species seems to occur in tropical and subtropical regions (*sensu* Brown 1987), where birds live in stable (i.e. predictable food sources and climate) saturated habitats, with few possibilities for migration. Such habitats are especially found on small tropical islands. The absence of co-operative breeding in *Acrocephalus* species at temperate latitudes could be explained by the fact that these are non-resident, migratory species with high adult mortality and, hence, increased population turnover (Arnold & Owens 1998), thereby breaking up social relationships.

In this paper we first investigate whether co-operative breeding occurs in the African Reed Warbler (Fig. 1), a non-migratory, presumably isolated, continental species constituting a saturated population in a stable wetland environment. The African Reed Warbler occurs across the whole southern part of the African continent (MacLean 1984). In South Africa it is migratory, whereas in Namibia it is resident (R. Simmons pers. comm.), breeding in small reed patches along the coast. These patches are essentially islands, separated by harsh, dry, inhospitable desert. The species exhibits a meta-population structure, with some movements between nearby sites (< 35 km), but no exchange between more remote areas (> 70 km; Eising *et al.* unpubl. data). Considering the species' isolated habitat and the lack of territory vacancies (Eising *et al.* unpubl. data) we expect to find co-operative breeding to some extent. Secondly, we investigate the general breeding ecology of the African Reed Warbler, of which very

Figure 1. The African Reed Warbler.

little is known even though the species is common, and determine whether habitat characteristics can be linked to the occurrence of co-operative breeding.

METHODS

Study sites and species

During the periods September to December 1995 and August 1996 to January 1997, African Reed Warblers were observed and caught in eight reed patches along the coast in Namibia (Fig. 2). The study areas at Walvis Bay (WB, 20.0 ha) and the Swakopmund Sewage Works (SSW, 1.3 ha) were situated in local sewage works, whereas the Swakopmund River (SR, *c.* 40.0 ha), Swakopmund Lagoon (SL, 3.4 ha), Henties Bay (HB, 0.3 ha), Ugab River (UG, 1.0 ha) and Huab River (HU, > 30 ha) were situated in river mouths. Sandwich Harbour (SH, 1.8 ha), which was situated in a coastal brackish lagoon 50 km south of Walvis Bay, was the most southern study site. Sandwich Harbour and Walvis Bay were separated by sand dunes. The Swakopmund area (comprising SSW, SL and SR) near Swakopmund, was 35 km north of Walvis Bay. Each area was separated by 5 km of suburban gardens and small desert patches. Henties Bay, 70 km north of Swakopmund, was separated from the Swakopmund area by dry, harsh desert without any vegetation, as was the Ugab site (UG) 130 km north of HB. HU lay 40 km of bare desert north of UG.

There was little exchange between the warbler populations living in the Swakopmund area, Walvis Bay and Sandwich Harbour. Only 22 out of 821 individuals (2.7%) were known to have moved between these sites. There was no migration into these populations from warbler populations ringed elsewhere (0 out of 57 individuals, Eising *et al.* 2001.). Observations on the African Reed Warblers' breeding ecology were restricted to the Walvis Bay area for logistic reasons. All study sites consisted primarily of Reed *Phragmites australis* interspaced with Reedmace *Typha latifolia*.

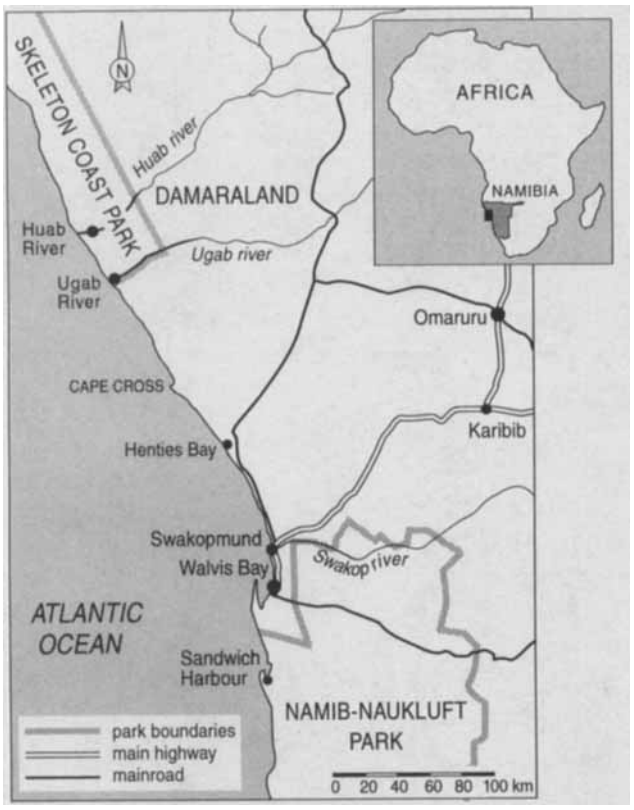

Figure 2. Map showing the location of the study sites along the Namibian coast. The study sites Swakopmund Sewage works and Swakopmund Lagoon are located at Swakopmund.

Data collection

Warblers were caught by mist-net. Each bird was ringed with a metal ring (Safring, Capetown) and a site- and individual-specific colour ring combination. All birds were checked for presence of a brood patch and a blood sample (*c.* 20 µl) was taken from the brachial vein in adult birds, and from the tarsus of nestlings (at least 4 days old). The blood samples were stored in dimethylsulfoxide buffer and used for sex determination and DNA fingerprinting analyses (see below).

Nests were typically built in sturdy, brown, but not dead, vertical reed stems. They were found within the reed beds by systematically searching along parallel transects 2 m apart. Nests that were empty or contained one egg were checked daily to date any further eggs and determine the completion of the clutch. All eggs were marked with an indelible marker. Every other day clutches were checked for hatching. Young were marked with an indelible marker on their beaks until they were old enough to be colour-ringed. Nestlings were weighed every other day.

Video recordings were used to score the number of adults involved in breeding behaviour (67 nests), incubating (32 nests), brooding (15 nests) and food provisioning rates of young (22 nests). Cameras (Hitachi Hi8) were set up within 1–3 m of the nest, and nests were recorded for a minimum of 60 minutes. Most nests were recorded between two and five times as the eggs hatched and nestlings matured to determine the investment of each adult in incubation and

food provisioning and to observe changes in provisioning rates of young as they grew. Nests were monitored between 07:00 h and noon, after which it became impossible to identify the colour-rings due to sun glare.

Reed patch quality

At Walvis Bay, territory size (ha) was assessed by observing the territory holders' movements and aggression towards neighbouring warblers. During the breeding season, warblers defended exclusive territories. Since the African Reed Warbler is purely insectivorous (MacLean 1984), habitat quality was not only assessed by measuring reed parameters, but also using measures of insect availability. A transect was chosen through the study area, along which 1-m^2 quadrats were scored at 10 m intervals. Average reed height (m), reed diameter (mm), density of stems (no./m^2) and the proportion of live green, live brown and dead reed was scored in each quadrat. These are referred to as non-nest transects. An extra transect was selected in the vicinity of the nest (nest transect) to define nesting preferences.

Insect prey abundance was determined by using water traps with detergent. This method has the highest correspondence with the prey spectrum of *Acrocephalus* species (Hoi & Ille 1997). All traps were dark green, 13.5 cm in diameter, and were filled with water and detergent to a depth of 2.5 cm. The measurements were taken on dry days with an estimated wind force less than 3 on the Beaufort scale, repeated once a week throughout the study period, and were continued after a nest had successfully fledged young. In 11 randomly chosen territories, three traps were set out for 24 hours at a height of 1.3 metres, 2 m from the nest. Totals of the following groups were counted: Diptera, Arachnidae, Coleoptera, Formicidae, Isoptera (Termites), Hymenoptera, Hemiptera and Lepidoptera. Insect prey availability was expressed as the mean number of insects caught per day within a territory, multiplied by the average height of the reed and territory size. The body lengths of insects were classified into the following categories: 0 – 2.0 mm, 2.1 – 4.0 mm, etc. Insect mass per territory was calculated as the product of four terms: the number of insects caught within a certain category, the median length of insects in that category, territory size and reed height.

Wind exposure of nests was measured as the difference between two anemometers, one placed in the open (control cup) and one close to the nest (experimental cup). The difference in wind speed between the control and experimental cup was plotted against the control wind speed and regression coefficients calculated for each nest-site. These coefficients are referred to as the wind factor at each nest.

Sex determination and DNA fingerprinting

DNA was extracted following Sambrook *et al.* (1989) from blood samples collected from co-operatively breeding birds and their offspring. The sex of these birds was determined using the molecular sexing method developed by Griffiths *et al.* (1996). Samples were analysed using standard multi-locus mini-satellite DNA fingerprinting following Bruford *et al.* (1998). DNA was digested with HaeIII and probed with radioactively labelled 33.6 and 33.15 (Jeffreys *et al.* 1985). Fingerprints were scored following the methods outlined in Bruford *et al.* (1998). Banding patterns between helper/pair female dyads, helper/pair male dyads and unrelated individual dyads were calculated and compared. The pair birds were run in lanes adjacent to the helpers. In each case the band sharing coefficient was calculated based on the formula $S = 2N_{ab}/(N_a + N_b)$, where N_a and N_b are the number of bands present in individuals a and b, respectively, and N_{ab} is the number of bands shared by a and b (Wetton *et al.* 1992, Bruford *et al.* 1998). In cases where both pair birds at the nest were sampled we also determined the number of novel bands present (i.e. bands present in the helper/unrelated bird but not observed in either of the pair birds).

Data analyses

Data were analysed using both parametric and non-parametric tests. Tests are two-tailed and null hypotheses were rejected at $P < 0.05$. Significant P values were adjusted using the sequential Bonferroni correction (Rice 1989). Means are expressed with standard deviations unless stated otherwise. Percentages were arcsine transformed prior to testing.

RESULTS

Spatial distribution in the Walvis Bay area

Males were observed singing while foraging through the reeds, not from fixed song posts. Nests were found throughout the whole study area but data on territory size could not always be obtained because of the inaccessibility of the reed bed. Territory size was on average 335 m^2 (± 36 m^2; n = 27). Within this area

Table 1. Breeding parameters of breeding pairs and trios (breeding pair and one helper) of the African Reed Warbler.

Productivity	Pairs	Trios	Statistics	*P*
Average clutch size	2.3 ± 0.1 (n = 59)	2.2 ± 0.2 (n = 6)	$t_{63} = 0.30$	ns
No. of days between subsequent eggs	1.0 ± 0.0 (n = 13)			
No. of days of incubation	12.8 ± 0.4 (n = 25)			
No. of days till fledging	12.3 ± 0.3 (n = 9)	12.0 ± 0.7 (n = 2)		
Eggs hatching in nests with two eggs (%)	40.3 ± 6.8 (n = 36)	100.0 ± 0.0 (n = 4)	$U_{40} = 18$	< 0.01
Eggs hatching in nests with three eggs (%)	40.0 ± 11.4 (n = 15)	66.7 ± 0.0 (n = 1)		
Fledging in nests with two eggs (%)	27.8 ± 6.7 (n = 36)	50.0 ± 28.9 (n = 4)	$U_{40} = 56$	ns
Fledging in nests with three eggs (%)	15.4 ± 10.4 (n = 13)			

there were no vacant reed patches and territory borders were strongly defended against intruders and therefore distinct. If territory sizes were similar throughout the area, then the 20-ha Walvis Bay area could contain at least 600 territories. With an average breeding party of 2.12 individuals (see below), the estimated breeding population is estimated at 1270 birds.

Reproductive performance and co-operative breeding

From 1 September 1996 to 21 January 1997, 107 active nests were found in the study area. Of these nests, 12 contained one egg that never hatched and no breeding activity was observed near these nests. In 30 nests the eggs had already hatched. All other nests contained two (n = 46) or three eggs (n = 19). In 57 (88%) of the 65 nests that were filmed only the breeding pair was observed at the nest (referred to as pairs), whereas in the other eight nests an additional adult bird participated in breeding activities (referred to as trios). These 'helpers' were mature since they lacked the black tongue spots of juveniles (Svensson 1984). They were never observed incubating (n = 8 nests), but all were observed either brooding (n = 3) or provisioning nestlings (n = 6). One helper was observed brooding as well as provisioning the nestlings.

The breeding parameters collected for nests of pairs and trios are summarized in Table 1. There was no effect of laying date on clutch size (F_{35} = 1.33, ns). There was also no difference in clutch size and average number of days nestlings spent in the nest between nests of pairs and trios. Mean clutch size was 2.3 ± 0.1 eggs (n = 65). Eggs were laid one day apart. Eggs hatch after 12–13 days of incubation, and young fledge after 12–13 days. The number of adults attending the nests significantly influenced hatching success (Fig. 3). For two-egg clutches hatching success was significantly higher in trios than in pairs. In addition, hatching success for three-egg clutches is higher for trios than for pairs, but this could not be tested for significance due to the small sample size. For pairs, there was no signif-

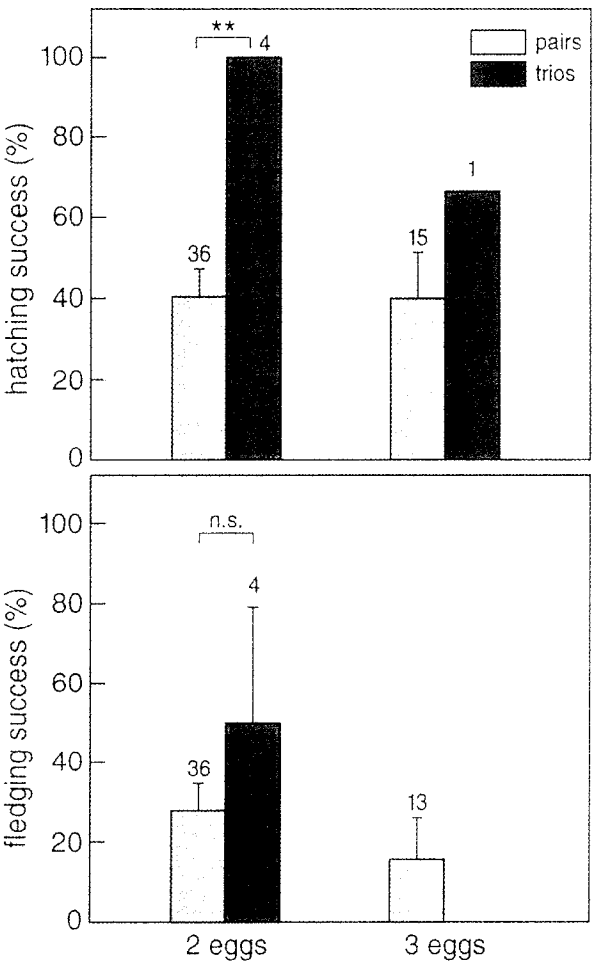

Figure 3. Hatching success and the percentage of eggs resulting in a fledgling in nests with two or three eggs for pairs and trios. Hatching success is calculated as the fraction of the original clutch that hatches. Top figures are sample sizes.

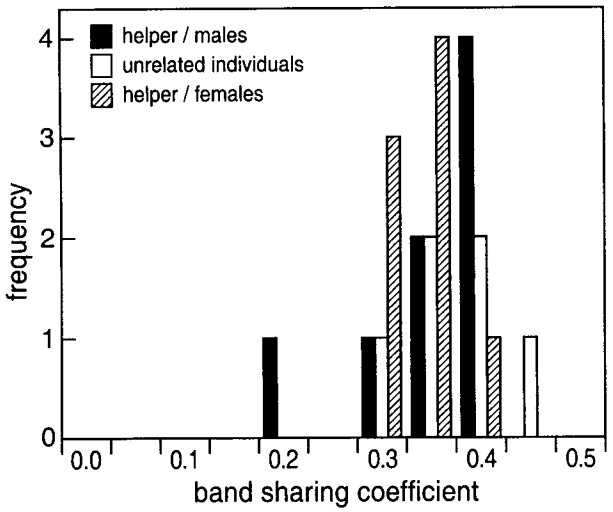

Figure 4. A histogram of the bandsharing coefficients of helper/pair male, helper/pair female and unrelated individual African Reed Warblers.

icant difference in hatching success between two- and three-egg clutches (Mann–Whitney U_{51} = 275, ns). The average hatching success with three adults was 93.3 ± 5.8%, whereas the average hatching success with only the breeding pair was 41.5 ± 6.7% (U_{56} = 40, $P < 0.01$). Hatching success over all nests was therefore low, 46.1 ± 5.4% (n = 56). The increased hatching success with three adults was not due to better incubation of the clutch (see below) but to lower loss rates of clutches (clutch loss: pairs: 49.0% (n = 51); trios: 0% (n = 5); χ^2 = 4.43, df = 1, P = 0.035).

Band sharing between parents and helpers

Band sharing coefficients did not differ significantly between helper/pair male dyads and unrelated individuals (0.35 vs 0.31; t = 1.51, df = 12, P = 0.16) or between helper/pair female dyads and unrelated individuals (0.32 vs 0.31; t = 1.51, df = 14, P = 0.65) (Fig. 4). There was no significant difference in the level of band sharing between helper/pair male and helper/pair female dyads (0.35 vs 0.32; t = 0.8, df = 12, P = 0.44; Fig. 4). Furthermore the helper always contained novel bands not present in either the pair male or pair female (x = 11.5 ± 4.1, n = 6). Therefore helpers do not appear to be related to either of the pair birds at the nest at which they help.

Fledging success and fledging weight

There was a significant negative correlation between the number of nestlings and time until fledging (r = –0.65, n = 9, $P < 0.05$). Single young stayed longer in the nest than young with one or two siblings. The average fledging success in two-egg clutches was not significantly different for pairs and trios (Fig. 3). Fledging success for three-egg clutches could only be determined in pairs. In pairs, there was no significant difference in fledging success between two- and three-egg clutches (U_{51} = 276.5, ns). The presence of a helper did not influence fledgling weight (Fig. 5a).

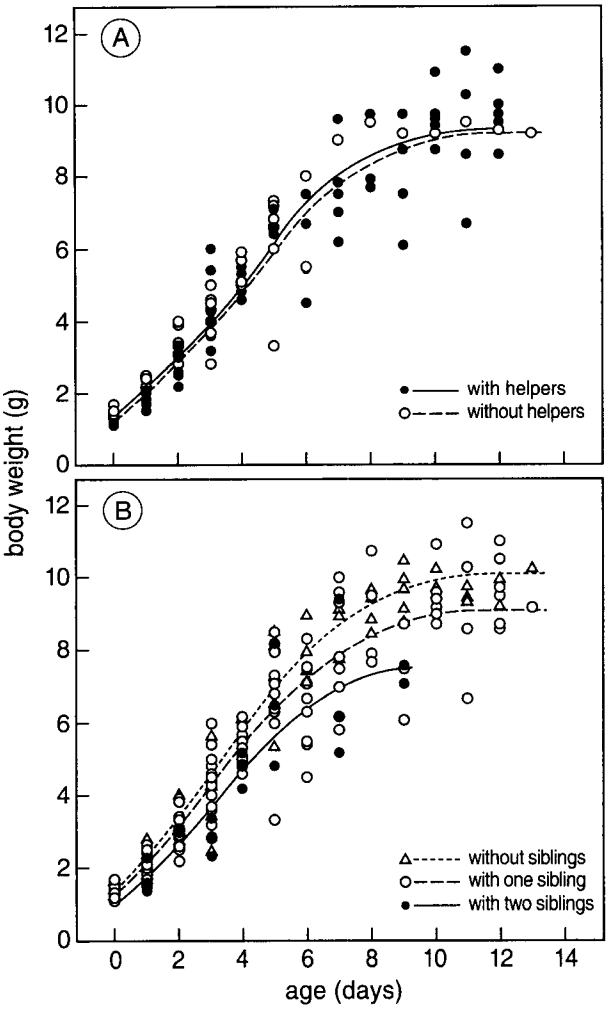

Figure 5. Growth curves for (A) young raised by pairs and trios and (B) single young, twins and triplets. Calculations were made for young between 2 and 10 days old, when growth is linear. The slopes of individual regression lines in A for young raised with or without a helper were not significantly different (t_{170} = 0.71, ns). The slopes of individual regression lines in B of single young, of young raised with one sib, and with two sibs were similar ($F_{2,38}$ = 0.125, ns). However, fledgling weight, corrected for day of fledging, was significantly higher for single young compared with twins or triplets (U_{44} = 332, $P < 0.05$ and U_{21} = 36, $P < 0.05$, respectively). There was no significant difference in fledging weight between twins and triplets (U_{27} = 35, ns).

Fledgling weight varied with brood size (Fig. 5b). Since there were no differences between young raised by pairs and trios all data were used in the analysis. The growth curves show that single young were heavier at fledging than young with siblings, and young with only one sibling were heavier than young with two siblings. The average fledgling weight for single young was 9.6 ± 0.5 g (n = 19), for young with one sibling 9.1 ± 1.3 g (n = 25) and for young with two siblings 8.0 ± 0.3 g (n = 2). The average fledging weight of single young was significantly higher than that of young raised with siblings (Fig. 5b). There was no significant difference in fledging weight between young raised with one and two siblings (Fig. 5b).

Division of labour: sex-specific reproductive performance

The sexes of individuals scored in the field (using observations on song and size of brood patch) all agreed with the sex determined later by DNA fingerprinting (22 males, 22 females). Breeding pairs always consisted of a male and a female (n = 12). The sex of the helper could be determined at four nests: three were male, one female. The helpers were not breeding birds from other territories. Thirty-two nests with eggs and young were recorded for a period of 120 minutes and the videotapes carefully analysed. On average, 58.2% of the total time was spent on incubation by the breeding pair. Eleven nests with two (n = 9) or three eggs (n = 2) were observed. At two of these nests an additional bird was seen (of which one was sexed as male), but these birds were never observed incubating. The average incubation bout lasted 5.42 minutes ± 0.31 (n = 11). Neither the percentage of incubation time nor the incubation bout length was dependent on the number of eggs (t_9 = 1.64, ns; t_9 = 1.41, ns, respectively). Both males and females incubated and the percentage of incubation time was similar for males (52.3%) and females (47.7%) (t_9 = 1.76, ns).

In 14 nests where brooding occurred, all adults at the nest could be determined: three nests with one young (one with helper), and 11 nests with two young (seven with helpers). Table 2 shows the fraction of time nestlings were brooded and Figure 6 shows the relative amount of time each adult invested in brooding in nests with and without a helper. The presence of a helper had no effect on the fraction of time nestlings were brooded nor on the average length of the brooding bout (Table 2, Fig. 6). Males and females appeared to invest equally in brooding. On average, helpers performed 9.7% of the brooding. This did not significantly influence the relative investment in brooding of either of the breeding pair members. Females in trios spent a similar time brooding to females in pairs (Table 2). The total number of feeding visits per hour did not differ between pairs and trios (Table 2). The food-provisioning rate was higher if there were two nestlings instead of one, both in nests with only the breeding pair and in nests with a helper (Table 2). This difference is signif-

Table 2. Brooding and food provisioning by African Reed Warbler breeding pairs and trios (breeding pair and one helper). The percentage of total time nestlings were brooded and the feeding frequencies (per hour) in nests with one or two nestlings, that were not assisted or were assisted by a helper, and the share of each adult bird in brooding and feeding the nestlings. The total percentage of time nestlings were brooded was not related to age of the nestlings (F_{13} = 0.44, ns) nor was the average brood bout length related to age of nestlings (F_{13} = 1.41, ns). For nests with two nestlings also the feeding frequency per young is presented. Food provisioning of nestlings was highly dependent on age of the nestlings (F_{37} = 14.70, P < 0.01). Food provisioning rates increased with increasing age of the nestlings. Therefore, all statistics are corrected for age-dependent effects.

	Pairs	Trios	Statistics	P
Brooding				
One young (%)	44.0 ± 5.2 (n = 15)	41.9 ± 5.4 (n = 3)	U_{18} = 24	ns
Two young (%)	42.4 ± 6.0 (n = 11)	49.0 ± 8.3 (n = 6)	U_{17} = 24	ns
Brood bout length (min)	6.1 ± 0.7 (n = 11)	5.8 ± 0.7 (n = 6)	U_{17} = 40	ns
Male brood share (%)	22.3 ± 13.5	51.8 ± 22.4	U_{10} = 8	ns
Female brood share (%)	77.7 ± 13.5	38.5 ± 18.8	U_{10} = 21	< 0.10
Helper brood share (%)		9.7 ± 4.5		
Feeding				
One young (h^{-1})	10.1 ± 4.0 (n = 11)	10.3 ± 2.7 (n = 6)	U_{17} = 37	ns
Two young (h^{-1})	14.6 ± 5.9 (n = 11)	12.6 ± 6.4 (n = 11)	U_{22} = 82	ns
Average per young (h^{-1})	7.3 ± 2.9 (n = 11)	6.3 ± 3.2 (n = 11)	U_{22} = 85	ns
Male feeding share (%)	50.3 ± 21.7	46.8 ± 38.9	U_{14} = 27	ns
Female feeding share (%)	49.7 ± 21.7	29.3 ± 26.0	U_{14} = 34	ns
Helper feeding share (%)		23.9 ± 22.2		

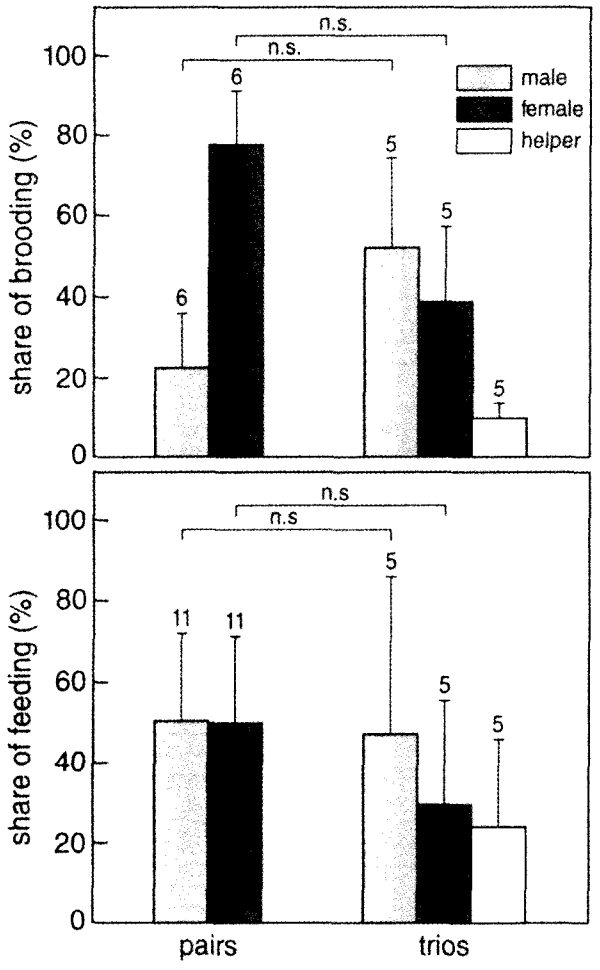

Figure 6. The share of each adult in pairs and trios in brooding and feeding of young. The difference between the change in brooding by the breeding female and the breeding male measured in pairs and trios was not significant ($F_{10} = 2.38$, ns). The difference between the change in feeding of young by the breeding female and the breeding male measured in pairs and trios was not significant ($F_{10} = 0.12$, ns). Top figures are sample sizes.

icant for breeding pairs ($U_{22} = 25$, $P < 0.05$), but not for trios ($U_{17} = 22$, ns). The feeding frequency per young in broods of two was significantly lower than the feeding frequency of a single young, both in nests of breeding pairs and nests with a helper ($U_{22} = 92$, $P < 0.05$; $U_{17} = 54$, $P < 0.05$ respectively). Feeding of nestlings was performed equally by males and females (Table 2, Fig. 6). Although females in trios were less involved in provisioning the nestlings than females in pairs, this difference was not significant. Helpers accounted for 23.9% of food provided to the nestlings. This was not significantly less than males or females did in trios ($t_{14} = 1.45$, ns; $t_{14} = 0.45$, ns, respectively).

Reed patch quality, nesting sites, and breeding success

Nests were found at an average height of 1.04 m (± 0.29 m, range 0.45–1.80, $n = 45$). The nest cups were made of reed fibres and lined with feathers, and were attached to several (2–7) small stems. Dead reeds were never used as a nest-site. The diameter of the inner and outer nest cup at the rim ($n = 30$) was on average 51.3 mm (± 2.7 mm) and 67.4 mm (± 4.2 mm) respectively. The reed parameters collected from nest and non-nest transects in 17 territories in Walvis Bay are summarized in Table 3. Reed stem diameter and reed stem density measured in all transects (both nest and non-nest transects) of the same territory did not differ between territories ($F_{14,17} = 0.69$, ns; $F_{14,17} = 1.25$, ns, respectively). The average reed height in transects of the same territory differed significantly between territories ($F_{14,17} = 4.25$, $P < 0.05$). All nests were found in the highest, densest and greenest patches of the territories (Table 3). The percentages of dead ($F_{14,17} = 3.24$, $P < 0.05$) and live brown reed ($F_{14,17} = 3.79$, $P < 0.01$) differed between the territories, but not between nest transects and non-nest transects (Table 3). The percentage of live green reed did not differ between territories ($F_{14,17} = 1.73$, ns), but was significantly higher in nest transects than in non-nest transects (Table 3). African Reed Warblers preferred high, dense, green reeds for nest building.

In the water traps, as much as 84.2% of the total number of insects caught and 73.9% of the total insect mass were Diptera and termites. Both insect abundance and insect mass were positively correlated with the percentage of live green reed in a territory ($r_{12} = 0.628$, $P < 0.01$; $r_{12} = 0.700$, $P < 0.01$).

Hatching success in pairs was significantly influenced by territory quality (Table 4). Hatching success was higher if reed stem density was higher or reed stem diameter was smaller. The effect of reed density and diameter on fledging success could not be determined due to lack of variance in fledging success. No effect was found of total insect availability per territory (insect frequency and insect mass) on hatching success or fledging success. Of 65 nests containing eggs, seven (11%) were destroyed after nights with strong winds (estimated wind force > 6 on the Beaufort scale). Wind exposure was directly measured at 11 nests. Wind exposure of nests had a negative effect on hatching success, but had no effect on fledging success (Table 4).

Table 3. Average reed stem height, reed stem diameter, stem density, percentages of dead, brown and green reed in nest transects and non-nest transects (± standard errors) in 17 African Reed Warbler territories in Walvis Bay. The statistics column presents the results of a MANOVA used to test differences between nest transects ($n = 17$) and non-nest transects ($n = 56$). After sequential Bonferroni correction only the parameter 'Reed height' remained significant ($\alpha = 0.008$).

Parameter	Nest transect	Non-nest transect	MANOVA	*P*
Reed height (m)	2.50 ± 0.41	2.06 ± 1.01	$F_{14,73} = 19.6$	< 0.01
Reed stem diameter (mm)	3.60 ± 0.19	3.70 ± 0.12	$F_{14,73} = 0.00$	ns
Reed density (no./m^2)	331.95 ± 19.21	248.24 ± 13.28	$F_{14,73} = 6.97$	< 0.05
% Dead reed (%)	53.24 ± 3.49	57.31 ± 2.25	$F_{14,73} = 0.55$	ns
Brown reed (%)	27.71 ± 2.73	27.84 ± 1.67	$F_{14,73} = 0.58$	ns
Green reed (%)	19.06 ± 2.08	14.84 ± 1.79	$F_{14,73} = 6.21$	< 0.05

Helpers and territory quality

Helpers were observed at eight out of 65 nests (12%). The presence of helpers, however, was not associated with any measure of territory quality (Table 5). Territories with and without helpers were similar in size, contained the same amount of insect food and same amount of dead reed and live reed. Nests of pairs with helpers were neither more sheltered nor built higher than nests of pairs without helpers. However, if all ten measures of territory quality were combined, territories with helpers were of significantly better quality than territories without helpers (Table 5). Eight of the ten measured territory quality parameters go in the predicted direction (Table 5).

DISCUSSION

The majority of African Reed Warblers breed monogamously (88%), however a small proportion of the population in Namibia breeds co-operatively with unrelated birds helping at the nest. The African Reed Warbler is not polygynous: (1) although the sample size is small, we have never observed that male helpers were actually breeding birds from other territories; (2) none of the breeding males attending nests have been recorded to provision nestlings at other nests ($n = 32$). African Reed Warblers have few opportunities to disperse to other areas and the habitat in and around Walvis Bay appears to be saturated (Eising *et al.* 2001). Territorial boundaries were vigorously defended against intruding neighbours and there appeared to be no vacancies in the reed area. Hoi *et al.* (1991) showed that the degree of inter-specific competition between three sympatric warbler species, the Great Reed Warbler, the Reed Warbler and the Moustached Warbler, influenced the expression of the breeding system. The polygynous Great Reed Warbler is dominant over the other warbler species, and occupies territories with the most abundant food, whereas the smaller, monogamous, Reed Warbler and Moustached Warbler occupy less rich territories. Given that Great Reed Warblers have more food available to feed their offspring than Reed Warblers and Moustached Warblers, male Great Reed Warblers are emancipated from feeding their offspring and have better opportunities to establish a polygynous breeding system. The African Reed Warblers do not suffer resource competition from closely related species. Other insectivorous species were captured in very low numbers within the reed beds ($n = 12$, 1.3% of all captures). Hence, it is unlikely that inter-specific competition influenced the

Table 4. The effect of reed density, reed diameter, insect availability and wind exposure on hatching and fledging success in African Reed Warbler pairs. There were no significant correlations between parameters and therefore all parameters have been tested independently. After sequential Bonferroni correction none of the five parameters was significant ($\alpha = 0.05$, number of tests is 5).

	Hatching success		Fledging success	
	Statistic	*P*	Statistic	*P*
Reed stem density (no./m^2)	$F_{1,13} = 7.76$	< 0.05	–	–
Reed diameter (mm)	$F_{1,15} = 6.81$	< 0.05	–	–
Insect availability	$F_{1,10} = 2.63$	ns	$F_{1,10} = 0.12$	ns
Insect mass	$F_{1,10} = 2.12$	ns	$F_{1,10} = 0.61$	ns
Wind exposure	$F_{1,11} = 5.62$	< 0.05	$F_{1,11} = 3.56$	ns

Table 5. Differences in African Reed Warbler territory quality parameters for breeding pairs and trios (breeding pair and one helper). Overall, territories of trios were of better quality than territories of pairs (sign test, $n = 10$, $P = 0.032$). Numbers between brackets are sample sizes.

	Territory of breeding pair	Territory of trios	Statistics	*P*
Territory size (m^2)	320 ± 170 (17)	492 ± 206 (8)	$t_{24} = 1.97$	ns
Wind factor	0.895 ± 0.026 (14)	0.949 ± 0.014 (3)	$U_{17} = 17$	ns
Insect abundance	14629 ± 3938 (9)	26119 ± 20480 (4)	$U_{13} = 22$	ns
Insect mass	34587 ± 9232 (9)	47418 ± 36605(4)	$U_{13} = 23$	ns
Average reed diameter (mm)	3.63 ± 0.21 (19)	3.40 ± 0.27 (4)	$U_{23} = 38$	ns
Average reed density	252.6 ± 11.9 (23)	275.0 ± 45.2 (4)	$U_{27} = 43$	ns
Nest height	1.019 ± 0.03 (29)	1.23 ± 0.12 (4)	$U_{31} = 29.5$	ns
Dead reed (%)	58.8 ± 2.4% (19)	46.1 ± 7.7% (4)	$U_{23} = 60$	ns
Live brown reed (%)	23.5 ± 2.0% (19)	35.9 ± 7.6% (4)	$U_{23} = 19$	ns
Green reed (%)	17.7 ± 1.4% (19)	18.1 ± 1.5% (4)	$U_{23} = 39$	ns

African Reed Warblers' mating system. Considering its population limitations, population isolation and apparent habitat saturation, there appear to be few opportunities for young birds to establish a territory of their own, and it is not surprising that the African Reed Warblers show co-operative breeding.

Co-operative breeding in the African Reed Warbler seems to be adaptive for the breeding pair, especially for the female. In nests with a helper, hatching success was significantly higher, although there was no significant difference in fledging success. The presence of a helper at the nest significantly reduces the amount of time spent brooding by the female, compared with that of the male. If helpers are genetically related to the breeding pair they can increase their inclusive fitness (Stacey & Ligon 1987, 1991, Emlen 1994). However, in the African Reed Warbler the helpers are unrelated to the breeding pairs and physically mature, and thus capable of independent reproduction. Even if helpers are not related to the breeding pair, helping may still be advantageous because of other benefits such as gaining breeding experience, increasing future breeding opportunities with a member of the breeding pair, inheriting a territory or receiving help in rearing their own young from the young they helped to rear (Emlen *et al.* 1991). The fact that in the African Reed Warbler only females seemed to benefit from the presence of a helper, and that three out of four sexed helpers were males, could indicate that some females are polyandrous. Unfortunately, the sex of the other four helpers could not be determined. In the Seychelles Warbler all helpers are related to one or both members of the breeding pair (Komdeur 1994b), whereas in the Henderson Reed Warbler helpers are not related to the breeding pair (Brooke & Hartley 1995). In the Seychelles Warbler natal philopatry is promoted because of differences in the territory quality of natal territories (Komdeur 1992). Birds raised on high quality territories are more likely to remain with their parents. The benefits of staying at home and helping to rear siblings are much higher than those of dispersing and starting an independent breeding attempt. In the African Reed Warbler no specific differences between territory quality of pairs and trios were found that might explain natal philopatry. However, overall, territories with helpers were significantly better in every aspect than territories without helpers.

Given the habitat saturation and the benefits of helping to the breeding pair and presumably to the helpers as well, it is rather surprising that helping occurred only in 12% of nests. In the Henderson Reed Warbler co-operative breeding was observed in 36% of nests (Brooke & Hartley 1995), whereas in the Seychelles Warbler the proportion of co-operatively reared broods, depending on the habitat quality, can be as high as 75% (Komdeur pers. comm.). In the African Reed Warbler only one floater was observed in the 30 studied territories, suggesting a general lack of potential helpers.

Two important ecological factors affecting reproduction in birds are nest-site quality (Martin 1992) and food availability (Ricklefs 1969). Vegetation density appears to be the most important determinant for nest-site quality, especially in open cup breeders (Martin 1992). In Walvis Bay, all nests were found in the highest and densest patches of the territories. Hatching success was higher if reed stem density was higher or reed stem diameter was smaller. These types of reed are presumably less accessible to predators. Wind exposure of nests reduced hatching success, but not fledging success. Presumably the eggs are more easily thrown out of a swaying nest than young warblers, which may hold on to the nest with their claws. This

agrees with other studies where reproductive success was determined by nest-site choice (Burger 1985, Wiens 1989, Ille & Hoi 1995). Food availability in the vicinity of the nest has a direct influence on the ease of raising offspring for the parents (Duckworth 1990, Westneat *et al.* 1990). In this sense, food access is very important in determining whether biparental care is necessary (Hoi & Ille 1996). African Reed Warblers defend exclusive food territories and both parents engage in provisioning young, which suggests that food is a limited resource. The chance of fledging young is small in the African Reed Warbler (26.4%, $n = 53$). Since this was the first year of study, the survival of fledglings until one year of age is not yet known. Hoi *et al.* (1995) showed that the male feeding component decreased with increasing food abundance in several *Acrocephalus* species. Our results suggest that warblers prefer to build their nests in green reed, where food availability is highest. It is peculiar that the African Reed Warbler lays clutches of two to three eggs if food limitation is a problem. In pairs, broods of three young fledge on average 1.83 young, whereas broods of one or two young fledge on average 0.47 and 1.26 young, respectively. This suggests that nestling survival is equal for all clutch sizes and not higher in smaller clutches. Since territories of trios were of significantly higher quality than territories of pairs, food limitation might be important for the occurrence of co-operative breeding in the African Reed Warbler.

The presence of a helper improved hatching success, not through better incubation but through reduced clutch loss. The presence of a helper did not result in a higher fledging rate. Young from assisted nests were not heavier at fledging and did not fledge sooner. Although the feeding rates of helpers were relatively high, the total feeding rates per hour did not differ between breeding pairs and trios. Therefore there seems to be no direct benefit to the young of the presence of a helper. Another advantage of having an additional bird at the nest is possible earlier detection of predators and assistance in predator mobbing (Komdeur & Kats 1999). The percentage of eggs that hatched was as high as 94.5% in helper nests and only 40.2% in nests without helpers, although helpers do not engage in incubation. Predators seem to be abundant. There are several species of small herons, many snake species and on two occasions Brown Rats *Rattus norvegicus* were caught. As much as 20% of all nests was lost due to predation.

In conclusion, the results of this study show that African Reed Warbler pairs occasionally allow unrelated birds to help at the nest, which increases hatching success of their clutches, while the benefits to these helpers remain to be established. Overall, the territories occupied by pairs with a helper are more profitable than territories without helpers.

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